Published in 2013. Canadian Journal of Forest Research. 43(12): 1092-1103.

TITLE: Root production of hybrid poplars and nitrogen mineralization improve following mounding of boreal Podzols

AUTHORS: Simon Bilodeau-Gauthier*, David Paré, Christian Messier, Nicolas Bélanger
* corresponding author

AUTHORS’ AFFILIATIONS AND ADDRESSES:

Simon Bilodeau-Gauthier [1]
Centre for Forest Research, Department of Biological Sciences, Université du Québec à Montréal, P.O. Box 8888, Stn. Centre-Ville, Montreal, QC, H3C 3P8, Canada.

David Paré
Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy, Québec, QC, G1V 4C7, Canada. Email: david.pare@rncan-nrcan.gc.ca

Christian Messier
Centre for Forest Research, Department of Biological Sciences, Université du Québec à Montréal, P.O. Box 8888, Stn. Centre-Ville, Montreal, QC, H3C 3P8, Canada; & Institut des Sciences de la Forêt tempérée (ISFORT), Université du Québec en Outaouais, 283 boulevard Alexandre-Taché, C.P. 1250, succursale Hull, Gatineau, QC, Canada, J8X 3X7. Email: christian.messier@uqo.ca

Nicolas Bélanger
Centre for Forest Research, UER Science et Technologie, Téluq, Université du Québec, 5800 Saint-Denis, Montreal, QC, H2S 3L5, Canada. Email: nicolas.belanger@teluq.ca

[1] Corresponding (and current) address: Simon Bilodeau-Gauthier. Chair of Silviculture, University of Freiburg, Tennenbacherstr. 4, 79106 Freiburg i. Br., Germany. Tel: +49 (0) 761 203 8628. Fax: +49 (0) 761 203 3781. Email: simonbgauthier@yahoo.ca

ABSTRACT

Successful establishment of fast-growing trees could depend on early root development and the access to belowground resources. Boreal podzolic soils present a distinctive vertical zonation where nutrient availability and the presence of plant roots decline sharply with depth. Mechanical soil preparation that modifies the vertical arrangement of soil layers creates microsites with improved physical conditions, but potentially lower nutrient availability. We compared the vertical distribution of proximal roots of young hybrid poplars in soil layers of mechanically prepared (by mounding) and unprepared microsites. We also evaluated the relationship between root distribution and the availability and mineralization of soil nitrogen. Hybrid poplar roots were less abundant in the surface organic layer of unprepared soils, whereas they proliferated in the buried organic layer of mounds. Total mineralized N was highest in the upper mineral layer of mounds, while it was similar between the buried organic layer of mounds and the unprepared organic layer. Altogether, mounding created conditions conducive to greater soil N mineralization, and greater production and vertical distribution of proximal roots. This possibly provided access to a larger soil volume and greater soil nutrient pools, which may explain the success of mounding in terms of aboveground growth of hybrid poplars.

Keywords: hybrid poplar, mechanical soil preparation, nitrogen, Podzol, root distribution.

1. INTRODUCTION

Early root development of the target species is a fundamental factor in the successful establishment of plantations, as it can favour juvenile tree growth and survival (Grossnickle 2005). Indeed, planted seedlings that root well in their first year may experience better growth the following year (Luoranen et al. 2006). However, early root development may be impeded by microsite conditions such as a water-logged (Knapp et al. 2008), dry (Morris and Lowery 1988; Teskey and Hinckley 1981) or compacted soil (Wolken et al. 2010), or competition for belowground resources (Balandier et al. 2007; Löf and Welander 2004). One notable way to improve the early root development could be through adequate soil management prior to planting, such as mechanical soil preparation (MSP).

MSP creates soil disturbance that can improve microsite conditions by modifying soil texture and soil water regime, increasing soil temperature (Löf et al. 2012), and reducing the levels of both above- and belowground competition (e.g., DesRochers et al. 2004; Nilsson and Örlander 1999). MSP usually has a beneficial impact on tree growth (Örlander et al. 1990). Long-term benefits of MSP on the growth of Scots pines (*Pinus sylvestris*) were observed by Örlander et al. (1996), even though the mechanically prepared soils had much lower C and N content. Similar observations were made regarding the juvenile growth of nutrient-demanding hybrid poplars (Bilodeau-Gauthier et al. 2011).

Mounding is a type of MSP whose purpose is “to create elevated planting spots free from water logging and with little vegetative competition” (Löf et al. 2012). It can improve soil drainage and aeration (Londo and Mroz 2001), increase soil temperature (Knapp et al. 2008), and decrease soil bulk density. In water-logged conditions, mounding can improve tree survival and growth (Kabrick et al. 2005), although in drought-prone conditions it may worsen the effects of soil drought (Hallsby and Orlander 2004). A certain number of studies have shown that mounding benefits the root system of planted trees (Bolte and Löf 2010, with *Quercus robur*; Knapp et al. 2006, with *Pinus palustris*). The decrease in soil bulk density, for instance, generally favors root development and growth, since a looser soil allows easier root penetration (Löf et al. 2012).

MSP can also modify the spatial distribution of soil nutrients, for instance by amalgamating nutrients in patches or redistributing the rich top layers into a greater soil volume. Plant root growth may show plastic response to nutrient-enriched soil patches, which may optimize root foraging and efficient acquisition of resources (Hodge 2004). However, there have been very few studies on the response of tree roots to the spatial distribution of soil resources (Hawkins and Metcalfe 2008, with *Pseudotsuga menziesii*; Heineman et al. 1999, with *Picea glauca*; Makita et al. 2011, with *Quercus serrate* and *Ilex pedunculosa*). Heineman et al. (1999), notably, studied spruces growing on mounds and they analyzed vertically the soil and tree root system. However, they delimited vertical sampling layers based on fixed depth intervals (as did Makita et al. 2011) rather than by soil horizon types as advocated by Strong and La Roi (1988). In this respect, their results cannot be used to identify root foraging strategies with regard to the optimal preference of soil material in which to proliferate.

Boreal forest soils (most notably Podzols, Luvisols, and Brunisols/Cambisols; IUSS Working Group WRB 2006; Soil Classification Working Group 1998) present two particular features that create a distinctive vertical zonation and in turn influence plant establishment and development. The first feature is that nutrient availability declines sharply with soil depth (Gastaldello et al. 2007; Paré and Bernier 1989), whereas this transition is much less abrupt in other soil types that have an active burrowing macrofauna (Wood et al. 1984). The second distinctive feature of boreal soils is that plant roots mainly colonize the first 15 cm of soil (Strong and La Roi 1983, 1985), which includes the organic layers and the top of the (mineral) B horizon, with roots avoiding or bypassing quickly the Ae horizon when present. In a review on the rooting pattern of boreal trees, Van Rees (1997) indicated that approximately 50% of the fine roots where within the organic layers, while Finér et al. (1997) found more than 80% of all roots in the 5-8 cm thick organic layer and the first 10 cm of the B layer (Strong and La Roi 1985). Brassard et al. (2013) showed for several boreal tree species that the number of fine roots was highest in the surface organic layer and dropped steadily with soil depth; for non-tree fine roots, the pattern was even more skewed towards the organic layer.

To better understand the relationships between tree root development and the spatial arrangement of soil layers (and available soil nutrients), we took advantage of a well replicated experimental design with hybrid poplars planted on podzolic soils of the southern boreal forest of Québec, Canada (Bilodeau-Gauthier et al. 2011), where soils either 1) were left unprepared or 2) received MSP by mounding. These two treatments allowed comparing a soil that follows the typical sharp vertical boundaries found in podzolic soils (the unprepared control) with a soil where this spatial pattern was disrupted (the mounding treatment). We chose hybrid poplars because of the generally high nutritional needs of *Populus* species (Paré et al. 2001) and clones (Mitchell et al. 1999), and because they often respond negatively to the presence of competitors (Kabba et al. 2007). Indeed, as shade-intolerant trees, they are known for their sensitivity to aboveground competition for light (Messier et al. 1998). Yet, as pioneer trees, hybrid poplars also seem to be intolerant of belowground competition for nutrients and space (Coll et al. 2007; Messier et al. 2009). Such a demanding tree may fare poorly when planted in soils with a distinctive vertical zonation such as Podzols, unless soil management prior to planting accounts for the soil's particular features and aims at creating improved conditions suited to the tree's needs.

We undertook root excavations within the aforementioned experimental plantations of hybrid poplars (Bilodeau-Gauthier et al. 2011). The main objective was to compare how the root system of hybrid poplars developed in the different soil layers of the two soil treatments. A secondary objective was to characterize soil nitrogen availability in the different soil layers of the two soil treatments. We hypothesized that the vertical distribution of hybrid poplar roots would reflect the improved soil conditions created by mounding, and that roots would respond to the nitrogen availability in the different soil layers. A previous experiment under controlled conditions had suggested that root development of hybrid poplars was particularly sensitive to soil conditions (Messier et al. 2009), and soil N is the most limiting nutrient in boreal systems (Fisher and Binkley 2000) where N additions were often shown to improve tree growth (Newton and Amponsah 2006). The results should help increase our understanding of the response of hybrid poplar trees to the spatial distribution of soil resources, as well as improve the efficiency of silvicultural treatments such as soil management.

1. METHODS

2.1 Sites and experimental design

This study took place among experimental plantations that are described elsewhere in greater details (Bilodeau-Gauthier et al. 2011). Eight formerly forested sites were chosen in the Saguenay–Lac-St-Jean region (southern boreal forest, between 71° 05' and 72° 52' W, and between 48° 08' and 48° 43' N) of the province of Quebec, Canada. Tree species in original stands consisted of balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), and paper birch (*Betula papyrifera*). Soils are representative of Precambrian Shield settings characterized by coarse acidic soils (soil texture: 70% sand, 25% silt, 5% clay; mean pH of the B horizon = 4.1, SD = 0.2), and are classified as Orthic Ferro-Humic Podzols (Soil Classification Working Group 1998). All sites were found on moderate slopes with no apparent waterlogged conditions, thus classified as mesic with a good drainage (volumetric water content: 14% in mounds, 26% in unprepared soil). A description (thickness and depth) of the different soil layers is provided in Table 1, where the unprepared treatment is representative of natural conditions. Mean annual temperature for this region is 2.2°C and mean annual precipitation is 1000 mm (of which 710 mm is rainfall), while mean summer (June-September) temperature is 15.5°C and mean monthly summer precipitation (rainfall) is 107.5 mm (Environment Canada 2009).

Following whole-tree harvesting in the summer of 2002, soils were mechanically prepared in the fall of 2003. Two soil treatments were compared: 1) MSP by mounding and 2) a control where the soil was left unprepared. Each treatment covered a 1 ha plot and was repeated at each of the eight sites, hence $n = 8$. The 1 ha plots were further divided into four equal subplots (0.25 ha) where different vegetation control (weeding by brushing) schedules were tested. The data presented here was obtained from the subplot with the most frequent weeding schedule (vegetation controlled once a year during the first 3 years). Bare-root, ~ 1 m tall hybrid poplar tree cuttings of the 915319 clone *Populus maximowiczii* × *Populus balsamifera* (Périnet et al. 2001) were obtained from a nursery operated by the Ministère des

Ressources naturelles et de la Faune du Québec at Grande-Piles, QC, Canada. The cuttings were produced in the spring from stool beds in the nursery plantations, and cultivated over the summer in irrigated, fertilized, and weeded soil. This allowed them to develop a substantial root system, which was subsequently groomed in the fall when the cuttings were dormant, a state in which they were kept until shipped to the field the next spring. Bare-root cuttings were hand-planted with a shovel in April 2004 at a depth of 20-30 cm and in straight rows at a spacing of 3 × 3 m (density = 1100 trees ha^{-1}). The year of planting is hereafter considered as year 1. Tree cuttings were planted on the side of the mound, down to a depth of 20-30 cm so that the rooted end of the tree cutting reached at least the buried organic layer. Trees in the unprepared control were planted at the same depth as those on mounds (when possible, since unprepared soil was not as easily penetrated as the soil of mounds, see Bilodeau-Gauthier et al. 2011). Figure 1 provides a schematic description of mounding and Table 1 illustrates the vertical soil profile of the two treatments.

Mounding is a common MSP treatment in Scandinavia and Canada (DesRochers et al. 2004; Örlander et al. 1990; Sutton 1993). For this study, it was done using a backhoe equipped with a 45 cm wide bucket that dug into the soil through the organic layer (also called LFH in the Canadian Soil Classification, or O horizon in the World Reference Base for Soil Classification) and down to a depth of 60 cm to retrieve the mineral soil (i.e., the B horizon, which, in the case of Podzols, is visually, physically, and chemically very different from the soil layers located above it: the organic layer composed of organic matter in different states of decomposition, and the Ae horizon enriched in minerals recalcitrant to biochemical weathering such as quartz and muscovite). The mineral soil and the organic layer were then upturned over undisturbed soil nearby to form a mound of about 30 cm in height and 50 cm in radius. This mound therefore covered the vegetation that had regenerated after the harvest. The resulting combination of undisturbed and upturned organic material – hereafter referred to as the buried organic layer – found within mounds (Figure 1) was compressed by the mineral soil over it so that it was thinner than the undisturbed organic layer (Table 1). Bilodeau-Gauthier et al. (2011) reported that the upper part of mounds (composed of mineral soil) presented, compared with the upper part of unprepared soils (composed of organic matter), a lower soil bulk density (measured as higher penetrability), lower total soil N concentrations (mounds: mean = 0.8 mg g^{-1}, SE = 0.2; unprepared: mean = 3.4 mg g^{-1}, SE = 0.6), and a higher soil temperature (mounds: mean = 14.8°C, SE = 0.9; unprepared: mean = 13.8°C, SE = 0.5).

2.2 Root excavations

In July of year 4, 45 three-year-old hybrid poplar trees were randomly chosen in the mounding treatment (24 trees, three per site across the eight sites) and the unprepared control (21 trees, three per site at seven sites, as one site had no usable control). The root system was partly excavated in a non-destructive manner. Digging was done by hand in a 30 cm radius around the base of the trees and down to the cutting end (see maximum rooting depth in Table 1). Such partial excavations allowed us to maintain the tree stability and spatial arrangements of roots. The excavation process exposed all roots that started directly from the poplar cutting itself. These roots are called proximal roots in the literature (Domenicano et al. 2011); one could think of them as main, primary or first-order roots (e.g., Fitter 1986; Rose 1983) that can be of any size and that subsequently branch into several smaller roots.

Diameter at the base (at the junction with the cutting, also called the root collar) of every proximal root was measured with an electronic calliper. The use of the proximal root diameter was based on a positive demonstration by Domenicano et al. (2011) that proximal root diameter of hybrid poplars was strongly and linearly related to other root characteristics. These authors undertook complete excavations of root systems and made numerous measurements of root architecture and physiology. They successfully built linear equations ($R^2 = 0.6$ to 0.8, $P < 0.0001$) linking proximal root diameter to root length, root biomass, and number of root links, thus suggesting that non-destructive, partial excavations were an adequate proxy for total root biomass and architecture. Moreover, they excavated root systems from 2-year-old hybrid poplars of clone types (913313 and 913311, both *P. maximowiczii* × *balsamifera*) that are closely related to the clone used in the present study.

The depth (from the soil surface) at which a proximal root was located was noted with a measuring tape. The fact that the hybrid poplar cuttings were planted deep into the soil, as well as their capacity to produce roots from the whole length of the cutting that is belowground and not just the already-rooted bottom end, meant that proximal roots extended relatively horizontally from the cutting – at least in the 30-cm radius area that was sampled –, which simplified the identification of the soil layer which was explored. Thickness and location of the organic and mineral soil layers were also noted for every tree (which was made possible by the clear visual horizonation of Podzols) to later build an average vertical soil profile for each treatment (Table 1). After measurement, the soil was gently filled back in to cover the roots. Total stem height and annual shoot lengths of the 45 excavated trees were measured with a measuring pole and tape. Stem diameter was measured with an electronic calliper, at mid-breast height (65 cm from the ground) because some trees were too short to allow measuring at the standard height of 1.3 m.

For every tree, the sampled proximal roots were subsequently classified by diameter (0-2, 2-10, 11-20, and 21-30 mm) and by the soil horizon in which they were found. Roots will thereafter be mainly referred to according to their diameter class, rather than to other common terms like “fine roots” or “coarse roots”. Such terms imply that the function of said roots is known, which is not necessarily the case since the link between root diameter and function may vary between species. Calculations were made for average diameter of proximal roots per tree, number of proximal roots per tree and per diameter class, and absolute number of proximal roots per soil layer (organic and mineral soil). The relative abundance of roots per cm of soil depth was obtained by dividing the absolute number of roots per tree per soil layer by the average thickness of the soil layer. The ratio of tree height over root surface (this denominator being the product of average root diameter and total number of roots of a tree), thereafter referred to as the height:root ratio, was also computed.

2.3 Soil analyses

In situ soil incubations served in assessing potential net N mineralization. To this end, nitrate (NO_3) and ammonium (NH_4) concentrations were compared between the start and the end of 6-week (from the beginning of July to mid-August) *in situ* incubations undertaken at two (for the unprepared control) or three (for the mounding treatment) different soil depths, i.e., 0-15 cm, ~20 cm, and for mounds also ~30 cm. Soil samples were taken at a distance of 30 cm from the base of three trees per soil treatment at each site (overall: 45 trees, 114 incubations, n = 8 for mounding and 7 for the control). These trees were not the same that were excavated for root measurements. The 0-15 cm incubations were conducted in year 4 with 20 cm long and 5.8 cm wide closed-top PVC tubes as described in Raison et al. (1987) and Brais et al. (2002). The initial soil samples were obtained by inserting the tubes into the surface soil and taking back this volume of soil immediately to the laboratory. At the same time and at the same distance from the tree, but not in the exact same spot, other tubes of equal dimensions were inserted into the soil and left in place for the 6-week duration. The ~20 and ~30 cm incubations were done in year 5 at the same distance from the same trees that were used for tubes. Initial soil samples were obtained by extracting with a soil auger about 1 kg of soil material from each depth. Final soil samples were obtained by extracting a similar quantity of soil at the same depths, placing it in polyethylene bags and burying it back in the holes under the soil material that had been taken out (note that the ~20 and the ~30 cm incubations were not placed directly one above the other). Bags were tightly closed to prevent leaching induced by percolating waters (Brais et al. 2002). Soil incubations provide an estimate of the soil potential for net N mineralization. Being mostly closed to outside influences that could alter nutrient concentrations (e.g., water flow, root uptake), yet subjected to *in situ* temperature conditions, incubations constitute a snapshot of the activity of the microorganisms that degrade soil organic matter, which releases N into inorganic forms more readily accessible to plants (mostly NH_4, in the type of soils studied here) during the most active period of the year. For all tube and bag soil samples, NH_4 and NO_3 were extracted from fresh soil with 2M KCl (Maynard et al. 2007) and analyzed by flow injection analysis and ion chromatography (FIA; Lachat Instruments, Milwaukee, WI).

Potential nitrogen mineralization was calculated as the difference in the inorganic N measurements between the final and initial incubations. The amount of mineralized N was further estimated for the total soil volume. This volume differed between the two treatments. It was schematically represented as a cylinder with a 50-cm radius surface area (the size of a mound) and a length corresponding to the location of the deepest proximal root (see Table 1). From the vertical soil profiles, it was possible to calculate a volume for each soil layer. The density of the mineral layers was obtained from the calculations of Saxton et al. (1986), using a soil texture of 70% sand, 25% silt, and 5% clay (data taken from Bilodeau-Gauthier et al. 2011); this was done because the mineral soil was often too rocky in those sites and our standard method of using a small sample tube of known volume was not feasible. The density of the organic layer was derived from surface soil samples taken in plots of the unprepared control with incubation tubes of known dimensions (in these plots, the tube samples were mostly comprised of organic soil material). By combining the total volume of soil per layer with the density of each layer, a total mass of soil per layer was calculated. Afterwards, N values per soil mass unit were related to total mass of soil per layer to provide a total quantity of N for the whole soil profile.

In addition, soil concentrations of NO_3 and NH_4 were assessed in year 5 with ion-exchange resins (Plant Root Simulators, or PRS^{TM}-probes, Western Ag Innovations, Saskatoon, SK, Canada). The ion-exchange resin of these probes is a thin membrane (1.5 cm × 5.5 cm in surface area) contained in a small plastic probe (3 cm × 15 cm) that can be inserted into the soil with little disturbance. Resins were vertically installed at three soil depths, i.e., 0-5 cm, ~20 cm, and ~30 cm, during the same 6 weeks and at the base of the same trees as the incubations. During the burial period, the resins continuously adsorb soil nutrient ions that are flowing to the probe through the soil solution. The amounts of nutrients trapped by the resin represent the nutrient supply rate from freely flowing water to a specific soil location within the soil profile during a specific burial time period. It is a dynamic measure of ion fluxes in the soil over time, rather than a static measurement at a particular point in time like more conventional extraction methods

(Qian and Schoenau 2002). Several previous studies in agronomy and forestry have successfully used PRS^{TM}-probes to assess soil nutrient availability (e.g., Adderley et al. 2006; Moukoumi et al. 2012).

Soil temperature was assessed with data-logging temperature sensors (Maxim Integrated Products, Sunnyvale, CA, USA) placed at the base of 15 trees from two out of the eight sites (9 trees on mounds, 6 trees in unprepared soils). Soil temperature was measured at depths of 2, 10 and 20 cm every 2 hours from the beginning of June to the end of October during year 4. A previous study on the same research sites (Bilodeau-Gauthier et al. 2011) had reported soil temperature values (see section 2.1) taken with a hand-held thermometer probe covering the same soil depth and over the same months, but only during the day.

2.4 Statistical analyses

Roots and soil data were compared between mounding and the unprepared control, as well as between the different soil layers; roots were further compared between root diameter classes. In order to illustrate the differences between all categories and combinations of variables, and because the soil treatment × soil layer interaction was incomplete (since mounding had three different soil layers while unprepared had two), we combined the soil treatments with the soil layers to produce a meta-variable with five levels (mound/upper-mineral, mound/organic, mound/lower-mineral, unprepared/organic, unprepared/mineral); for the roots data, this meta-variable further included the diameter classes (hence, a total of 20 levels). The meta-variable served as the fixed effect in mixed analyses of variance. The random variables consisted in plot (2 plots per site, each plot being in effect a soil treatment and containing 3 trees) nested in site (8 levels), which allowed to model the hierarchical design and thus use data from all sampled trees. Probability levels were resolved by Restricted Maximum Likelihood (REML; see Searle et al. 1992; Wolfinger et al. 1994). Data were also submitted to post hoc Tukey-Kramer HSD tests. Finally, non-parametric Spearman's rank correlations were conducted between root, stem, and soil characteristics for the 45 excavated trees. All statistical analyses used a confidence level of $\alpha = 0.05$ and were conducted using R 3.0.0 (R Development Core Team 2013).

3. RESULTS

3.1 Roots across the whole soil profile

When looking at all proximal roots across the whole soil profile of a tree, results showed that trees growing on mounds had a greater total number of proximal roots per tree compared with unprepared soils (respectively 35, SE = 2, and 25, SE = 2, at P = 0.006), but that the average root diameter was similar between the two treatments (respectively 5.1 mm, SE = 0.4, and 4.6 mm, SE = 0.4, at P = 0.4). Differences between soil treatments were also found among the different root diameter classes. Across the whole soil profile, the number of proximal 0-2 mm diameter roots did not differ between mounds and unprepared soils, whereas the number of proximal roots greater than 2 mm diameter was significantly greater in mounds (Table 2).

3.2 Roots across different soil layers

The most striking distinction between the two soil treatments was provided by the relative abundance of proximal roots (i.e., the number of proximal roots per cm of soil depth, used as a relative measurement of root density per soil layer) in the various soil layers (Figure 2 and Table 3). The 0-2 mm root diameter class in the buried organic layer of mounds had the highest relative abundance of all root diameter classes across all soil layers, except for the 0-2 and 2-10 mm classes of the unprepared mineral layer (Figure 2). For all treatments and layers, small roots (0-2 and 2-10 mm in diameter) were more numerous than large roots (11-20 and 31-20 mm), both in relative abundance (Figure 2) and in absolute numbers (Table 2).

Within the upper and lower mineral layers of mounds, the 0-2 and 2-10 mm diameter classes had similar relative abundances; between these two layers, the 2-10 mm classes were similar, but the 0-2 mm class had a higher relative abundance in the lower mineral layer (Figure 2). It must be noted, however, that the upper mineral was twice as thick as the lower mineral, which means that the absolute number of roots was actually higher in the upper mineral layer (data not shown). In unprepared soils, the mineral layer presented the highest relative abundance of proximal roots from all diameter classes but the largest (21-30 mm). Within each unprepared layer, the 0-2 and 2-10 mm diameter classes showed similar relative abundances (Figure 2).

The comparison of soil layers of similar material between the two treatments shows that proximal roots in the 0-2 mm diameter class had a higher relative abundance in the buried organic layer of mounds compared with the surface organic layer of unprepared soils. On the other hand, the underlying mineral layer of unprepared soils presented a higher relative abundance of proximal roots in the 0-2 and 2-10 mm diameter classes compared with the upper mineral layer of mounds, but similar relative abundances compared with the lower mineral layer (Figure 2).

3.3 Soil nitrogen and temperature

The ion-exchange resins installed at three different soil depths provided comparison between soil treatments regarding inorganic soil N availability, i.e., [NH_4+NO_3]-N (Figure 3a). At depths of 0-5 cm and ~20 cm, significantly higher values were found in the unprepared soils, more than two-fold the values observed in the mounds. Within a given treatment, N concentrations did not differ between depths, with the exception of mounding where significantly higher concentrations were observed at the ~30 cm depth. This depth was not sampled in the unprepared soils.

Potential net N mineralization was derived from the *in situ* incubations (Figure 3b). At 0-15 cm, the two soil treatments did not differ in net mineralized N over the 6-week period. At ~20 cm, net mineralized N was significantly higher in mounds compared with unprepared soils. In the latter, net mineralized N was significantly higher at 0-15 cm compared with ~20 cm. Conversely, in mounds, there was no significant difference in net mineralized N between 0-15 cm and ~20 cm, but it decreased significantly at ~30 cm. The calculation of total levels of net mineralized N in the soil rooting volume (Figure 3c) revealed that the upper mineral layer of mounds contained significantly more mineralized N than all other soil layers, thanks to its thickness and volume (Table 1). Within unprepared soils, greater amounts of total net mineralized N were found in the surface organic layer compared with the underlying mineral layer.

Soil temperature measured with data loggers was overall not significantly different between mounds and unprepared soils. However, when focusing on the three summer months (June to August) and discriminating for day and night temperatures, it was revealed that soil temperature at night was significantly higher in mounds (Table 4).

3.4 Above- *vs* belowground growth

The average total tree height in mounds was significantly greater than in unprepared soils (Table 5). Diameter at mid-breast height (mid-DBH) showed a similar difference. Estimated height:root ratio was significantly lower for trees on mounds compared with those in unprepared soils. Correlations between root, stem, and soil characteristics were tested for the 45 excavated trees (Table 6). Total number of proximal roots per tree was significantly correlated to the stem characteristics of tree height and mid-DBH. Tree height was also a strong determinant of the number of roots in all diameter classes. Mid-DBH was positively correlated to the number of roots per diameter classes, although the coefficients were greater for larger diameter roots (11-20 and 21-30 mm). Only these larger roots were significantly, and positively, correlated to soil temperature. Soil N characteristics did not correlate significantly to root variables. The height:root ratio was not correlated to any variable (data not shown).

4. DISCUSSION

4.1 Root growth in different soil layers

This study provided information on the distribution of proximal roots in various soil layers within a hybrid poplar’s immediate soil environment (30 cm radius around the base of the tree). This may hint at the preferential use of different soil material types in the early stages of the root system development, but it may not represent soil exploration beyond that area or in later years. One highlight of the results was the greater number of proximal roots of the 0-2 mm diameter class produced per cm of soil depth in the buried organic layer of mounds compared with the surface organic layer of unprepared soils (Figure 2), despite the fact that the buried organic layer showed lower resin-adsorbed N (Fig. 3a). The ratio of root production relative to resin-adsorbed N was thus much greater for hybrid poplars planted in mounds. In addition, given that the buried organic layer of mounds represented a lower proportion of the whole vertical soil profile than did the surface organic layer of unprepared soils, this preference suggests an advantage (e.g., improved nutrition) provided by mounding and by the burial of the organic layer (see next section on soil N).

This study also revealed enhanced colonization of the whole soil environment by hybrid poplar roots in mounds. Compared with trees planted in unprepared soils, trees on mounds produced a greater number of proximal roots, particularly larger roots. This is to be expected of trees with larger aboveground biomass, since large roots serve as anchorage (Coutts 1987). Yet, a proximal root branches into several additional, smaller roots, as reported by Domenicano et al. (2011) who showed that proximal root diameter was positively related to total root biomass and length. Hence, the larger proximal roots observed in mounds are also indicative of a generally more extensive root system.

Mounds likely provided advantageous conditions for root development, because of a higher soil temperature or lower soil bulk density (reported by Bilodeau-Gauthier et al. 2011) or other typical benefits of mounding mentioned in the literature (Löf et al. 2012). The present study showed that nighttime soil temperatures were particularly higher in mounds compared with unprepared soils, while daytime temperatures were comparable. The mounding process also possibly modified the physicochemical conditions of the buried organic layer due to the compaction of the organic matter (usually of low density and large pore size), therefore improving soil water holding capacity and aeration. These modifications, in turn, might have stimulated microbial activity and favoured mineralization of organic matter (see next section on soil N). Another benefit of the mound might have been to favour greater adventitious root formation – which is known to frequently occur in *Populus* species (Stettler et al. 1996) – along the whole length of the cutting and not only at its bottom end (where the roots formed at the nursery are found). Indeed, because of the looser soil of mounds, poplar cuttings may have been planted slightly deeper than in unprepared soils; consequently, a greater portion of the stem would have been in contact with the soil and might have produced a larger number of new adventitious roots.

Proximal roots from the 0-2 mm diameter class were found in equivalent numbers in mounds and unprepared soils. Yet in mounds they were mainly located in the buried organic layer. This layer may have offered more favourable conditions than the surface organic layer of unprepared soils: i) aeration may have been improved when this buried layer was somewhat compressed by the mounding process; ii) temperature may have been higher due to its position within the mound and its proximity with the warm upper mineral soil; iii) it may have contained fewer live roots from competing species, since these were buried and possibly killed during mound formation, which is a typical benefit of mounding, coherent with our field observation of a slow re-colonization of mounds by competing vegetation and also with previous studies reporting lowest vegetation covers on mounds, e.g., Knapp et al (2008); and iv) present results show that net N mineralization was high. In contrast, in unprepared soils, proximal roots in the 0-2 and 2-10 mm diameter classes were found more in the mineral layer, even though nitrogen mineralization was much lower in that layer compared with the surface organic layer, which suggests the unprepared mineral layer offered some other benefits to poplar roots.

Most plant species growing on boreal soils produce the majority of their roots in the surface organic layer or at the organic: mineral boundary (Brassard et al. 2013; Finér et al. 1997; Van Rees 1997); yet hybrid poplars in the unprepared soils of this study followed an opposite trend, with roots preferably growing in the underlying mineral layer despite its slower nitrogen dynamics. Previous studies have shown that the vertical distribution of fine roots may influence the outcome of competition between species, for instance by increasing the level of competition when species exhibit a similar root distribution (Bauhus et al. 2000). Species that are sensitive to root competition, e.g., pioneer tree species such as *Populus*, would therefore tend to avoid such a situation, a strategy called ‘competition avoidance’ (Novoplansky 2009) or ‘root segregation’ (Schenk et al. 1999). Hybrid poplars were shown to be sensitive to root competition (Coll et al. 2007), and even to avoid competing roots of other plant species (Messier et al. 2009). However, since competing roots were not directly quantified in this study, the results cannot clearly determine whether such a response to competition could have played a role in the advanced colonization by fine roots of the buried organic layer in mounds compared with the surface organic horizon of unprepared soils.

4.2 Soil nitrogen

The estimates of N mineralization obtained from *in situ* incubations indicated that concentrations of mineralized N in the surface layers of mounds and unprepared soils were equivalent. However, the unprepared soils experienced a stark decrease in net N mineralization with depth, whereas it remained similar between the surface mineral horizon and the buried organic layer of mounds (Figure 3b). This suggests that the disturbed soil conditions induced by mounding were at least as adequate, if not better as those of undisturbed soil to promote the release of N to tree roots via mineralization. A previous study done at the same sites showed that mounds had lower total C and N concentrations in the surface soil compared with unprepared soils (Bilodeau-Gauthier et al. 2011). If one were to compare net N mineralization (from incubation tubes, Figure 3b) with total N concentrations (see section 2.1), N mineralization in the upper mineral layer of mounds would represent a strikingly large part of total soil N, over 22%, whereas it would remain at 2 to 3% in unprepared soils. Moreover, when considering the volume occupied by each soil layer, the total amount of mineralized N in the upper mineral layer of mounds was strikingly higher than in all other soil layers (Figure 3c), thus pointing to the potential importance of this layer for nitrogen supply. In comparison, the buried organic layer, because of its thinness, had lower total net mineralized N than the upper mineral layer (Figure 3c), even though they had similar mineralization rates (Figure 3b). Nonetheless, the buried organic layer of mounds was not different from the unprepared organic layer, both in net and total mineralized N. Faster mineralization is important for tree nutrition during a given stand rotation, although it also raises the question of whether it could lead to long-term depletion of nutrient reserves (Örlander et al. 1996).

Because the upper mineral layer of mounds occupies a large volume, it appears to be the greatest contributor to total net mineralized N in mounds; meanwhile, for unprepared soils it is the organic layer that contributes the most. Since the total rooting volume is much larger in mounds, it would translate into greater total amounts of net mineralized N, all soil layers combined, compared with unprepared soils. This suggests that, even though N mineralization rates were at best comparable, and for some layers even lower, in mounds compared with unprepared soils, trees planted in mounds had access to greater nutrient pools thanks to soil conditions that favoured early root growth. Previous studies have similarly shown that MSP can favour tree development by favouring the exploration by roots of a large soil volume (Nadeau and Pluth 1997; Nordborg et al. 2006; Ross and Malcolm 1982).

Contrarily to the incubation results, the amounts of soil NH_4 and NO_3 adsorbed onto ion-exchange resins suggested that the soil N supply in unprepared soils was more than two-fold that in mounds, for all soil layers (Figure 3a). However, values from ion-exchange resins are affected by many microsite conditions. First, the ions absorbed by plant roots cannot be captured by the resin membrane. As hybrid poplar trees on mounds developed a larger biomass and a much larger root system than on unprepared soils, they may have been more efficient at absorbing available forms of N. Another possible explanation for the lack of concordance with incubations results is that the resins on mound may have lost their efficiency in capturing nutrients as they experienced desiccation due to summer drought conditions (Kjønaas 1999), and subsequent nutrient flows may have been underestimated in mounds.

The upturning of mineral soil to create the mound resulted in warmer and less compacted soil (Bilodeau-Gauthier et al. 2011), which is typical of mounding (Örlander et al. 1990; Sutton 1993). The increased temperature in mounds probably generated favorable conditions for the decomposition of the organic material within the buried organic layer and for the mineralization of N, by increasing the activity of microorganisms that transform organic N into mineral forms available for plant root uptake (Leirós et al. 1999). In addition, the burial of the organic layer may have compacted this otherwise much aerated organic material, which may have created better conditions for both soil N mineralization and root exploration. Also pointing to possibly favorable conditions of N mineralization are the available N amounts (as registered by ion-exchange resins) in the lower mineral layer of mounds, which were higher than the amounts in the overlying layers. This could reflect mineralized and newly available N from the buried organic layer that would have leached down the soil profile. It suggests that the organic layer could contribute to enriching the underlying mineral soil with N (and that, whether the organic material is buried or not, since the two unprepared layers also had similar resin-adsorbed N values). Nordborg et al. (2003) reported that net N mineralization was higher for MSP treatments that retained the organic layer in the planting microsite than when it was removed. They also showed that net N mineralization was positively correlated to root growth and N uptake. Therefore, it is possible that the hybrid poplars growing on mounds in the present study also took up more N. Similarly, in a study on MSP used for reforestation of *Pinus halepensis* in semiarid parts of Spain, Barberá et al. (2005) suggested that burying organic matter under furrows (rather than at the soil surface) may have contributed both to improve soil moisture conditions (as organic matter retained water) and to increase nutrient mineralization and availability (by favouring root access to nutrients), which might have led to better tree performance.

4.3 Hybrid poplar growth

Contrary to expectations, the height:root ratio was lower for hybrid poplars planted on mounds compared with those in unprepared soils. These results do not concur with previous work suggesting that smaller (or slower-growing) plants normally allocate more biomass to roots to obtain limiting nutrients (Cahill 2003), but they are in line with Pennanen et al. (2005) who found no increase in aboveground growth for 2-yr-old Norway spruces planted on mounds, but much greater root growth compared with trees in unprepared soils. In our study, a lower height:root ratio for hybrid poplars on mounds compared with unprepared plots did not proceed at the expense of stem growth. Indeed, the trees on mounds were actually taller than those in unprepared soils, suggesting that the larger root system that developed in mounds may have provided access to more available resources, and in turn actually increased the aboveground growth of hybrid poplars. In addition, if belowground competition was potentially higher in unprepared soils, then the smaller root system and higher height:root ratio of trees growing in unprepared soils might hint at some form of avoidance of the densely populated surface organic layer.

When planted in favorable conditions, juvenile hybrid poplars can easily outgrow other woody species and thus efficiently acquire light. However, newly planted trees often face harsh competition from herbaceous species, notably grasses, whose negative effect stems mainly from belowground competition (Collet et al. 2006). As such, early soil treatments such as mounding are very efficient for these species, which then require less control of the competing vegetation in subsequent years. Bolte and Löf (2010) thus suggested that mounding in *Quercus robur* plantations could offer an interesting alternative to herbicides, a suggestion that could be extended to other labour-intensive, time-consuming, or potentially environmentally-damaging vegetation control methods, or to mechanical methods involving intensive top soil displacements.

It is nevertheless conceivable that slower-growing species would respond differently to such management strategies. For instance, Boateng et al. (2009) showed that spruce (*Picea glauca*), which in the absence of silvicultural treatments was physically overtopped by vegetation, benefited more from lasting reductions in tall shrub and aspen abundance (i.e., increased light availability) than from early effects of mechanical soil preparation on the rooting microsite. Nevertheless, Cortini and Comeau (2008) observed that 11 to 13-year-old spruces were affected by surrounding woody shrubs in competition for light, but that herbaceous plants also had a detrimental impact on the growth of these trees via root competition, because of the spruces' shallow root system that put them in direct contact with herbaceous plant roots.

5. CONCLUSION

By burying the organic layer under a quantity of mineral soil, and thereby modifying the vertical arrangement of soil layers, mounds provided several nutritional and environmental advantages over unprepared soils. The advantages that were emphasized by this study focused on root distribution and nitrogen dynamics: First (1) the mounding process had positive effects on the net N mineralization, notably in the upper mineral layer of mounds (whereas the underlying mineral layer of unprepared soils had low N mineralization rates); Second (2) the burial of the organic layer that resulted from mounding seem to have benefited early root development, since this buried organic layer was extensively explored by the proximal roots of hybrid poplars; Third (3) proximal roots were overall more abundant in the mounds compared with unprepared soils, exploring a larger soil volume and thus accessing a larger nutrient pool (the total net mineralized N). Hence, our results suggest that mounding creates microsite conditions that favour N dynamics and early root development, which in turn enhances the aboveground growth of the planted trees.

This research has confirmed that the roots of fast-growing hybrid poplars, and likely other pioneer trees, are responsive to the spatial arrangement of soil layers and resources. This response may be explained in part by the sharp vertical zonation of podzolic boreal soils. Therefore, our results are likely to apply to soils showing a strong zonation, to soils devoid of a macrofauna mixing the soil layers, and to trees with a root system sensitive to soil conditions, for example fast-growing, shade-intolerant species. Soil management that aims at inducing a vertical rearrangement of soil layers in tree plantations may thus improve access to soil resources and optimize aboveground growth for fast-growing pioneer trees.

6. ACKNOWLEDGEMENTS

This study was funded by the “Fonds québécois de recherche sur la nature et les technologies” through a research grant to C. Messier et al. (project #2007-FO-118127), as well as a Ph.D. scholarship to S. Bilodeau-Gauthier. The authors acknowledge the participation of Louisiana-Pacific Corp., Chambord, QC division, notably C. Lavoie and M. Bonneau, in lending land and personnel for tree planting, and machinery for soil preparation. Other partners were the “Ministère des Ressources naturelles et de la Faune du Québec” (MRNFQ; P. Périnet and A. Fauchon for advice on poplar clones) and the Quebec Intensive Silviculture Network (RLQ; P. Gagné and B. Bigué for coordinating the project). Early contributors to the project include D. Cormier (FERIC), W. H. Hendershot (McGill University), P. Périnet (MRNFQ), and G. Prégent (MRNFQ). Western Ag Innovations (Saskatoon, SK, Canada) provided a discount on PRS^{TM}-probe analyses. Fieldwork assistance was provided by P. Gagné, L. St-Antoine (CFS), A. Beaumont, S. Reynolds, and A. Turgeon.

REFERENCES

Adderley, D.R., Schoenau, J.J., Holm, R.A., and Qian, P.Y. 2006. Nutrient availability and yield of wheat following field pea and lentil in Saskatchewan, Canada. Journal of Plant Nutrition **29**(1): 25-34. doi:10.1080/01904160500416430.

Balandier, P., de Montard, F.X., and Curt, T. 2007. Root competition for water between trees and grass in a silvopastoral plot of 10 year old *Prunus avium*. *In* Ecological basis of agroforestry. *Edited by* D. R. Batish, R. K. Kohli, S. Jose, and H. P. Singh. CRC Press, Boca Raton, FL, USA. pp. 253-270.

Bauhus, J., Khanna, P.K., and Menden, N. 2000. Aboveground and belowground interactions in mixed plantations of Eucalyptus globulus and Acacia mearnsii. Canadian Journal of Forest Research **30**(1): 886-1894. doi:10.1139/x00-141.

Bilodeau-Gauthier, S., Paré, D., Messier, C., and Bélanger, N. 2011. Juvenile growth of hybrid poplars on acidic boreal soil determined by environmental effects of soil preparation, vegetation control, and fertilization. Forest Ecology and Management **261**(3): 620-629. doi:10.1016/j.foreco.2010.11.016.

Boateng, J.O., Heineman, J.L., Bedford, L., Harper, G.J., and Nemec, A.F.L. 2009. Long-term effects of site preparation and postplanting vegetation control on *Picea glauca* survival, growth and predicted yield in boreal British Columbia. Scandinavian Journal of Forest Research **24**(2): 111-129. doi:0.1080/02827580902759685.

Bolte, A., and Löf, M. 2010. Root spatial distribution and biomass partitioning in *Quercus robur* L. seedlings: the effects of mounding site preparation in oak plantations. European Journal of Forest Research **129**: 603-612. doi:10.1007/s10342-010-0360-9.

Brais, S., Paré, D., Camiré, C., Rochon, P., and Vasseur, C. 2002. Nitrogen net mineralization and dynamics following whole-tree harvesting and winter windrowing on clayey sites of northwestern Quebec. Forest Ecology and Management **157**(1-3): 119-130. doi:10.1016/S0378-1127(00)00643-5.

Brassard, B.W., Chen, H.Y.H., Cavard, X., Laganière, J., Reich, P.B., Bergeron, Y., Paré, D., and Yuan, Z. 2013. Tree species diversity increases fine root productivity through increased soil volume filling. Journal of Ecology **101**(1): 210-219. doi:10.1111/1365-2745.12023.

Cahill, J.F., Jr. 2003. Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. Journal of Ecology **91**(4): 532-540. doi:10.1046/j.1365-2745.2003.00792.x.

Coll, L., Messier, C., Delagrange, S., and Berninger, F. 2007. Growth, allocation and leaf gas exchanges of hybrid poplar plants in their establishment phase on previously forested sites: effect of different vegetation management techniques. Annals of Forest Science **64**(3): 275-285 doi:10.1051/forest:2007005.

Collet, C., Löf, M., and Pagès, L. 2006. Root system development of oak seedlings analysed using an architectural model. Effects of competition with grass. Plant and Soil **279**(1): 367-383. doi:10.1007/s11104-005-2419-9.

Cortini, F., and Comeau, P.G. 2008. Evaluation of competitive effects of green alder, willow and other tall shrubs on white spruce and lodgepole pine in Northern Alberta. Forest Ecology and Management **255**(1): 82-91. doi:10.1016/j.foreco.2007.08.027.

Coutts, M.P. 1987. Developmental processes in tree root systems. Canadian Journal of Forest Research **17**(8): 761-767. doi:10.1139/x87-122.

DesRochers, A., Thomas, B.R., and Butson, R. 2004. Reclamation of roads and landings with balsam poplar cuttings. Forest Ecology and Management **199**(1): 39-50. doi:10.1016/j.foreco.2004.04.018.

Domenicano, S., Coll, L., Messier, C., and Berninger, F. 2011. Nitrogen forms affect root structure and water uptake in the hybrid poplar. New Forests **42**(3): 347-362. doi:10.1007/s11056-011-9256-x.

Environment Canada. 2009. Climate Data Online, Meteorological Service of Canada, National Climate Data and Information Archive. Available from http://www.climate.weatheroffice.gc.ca/links/index_e.html [accessed 5 December 2009].

Finér, L., Messier, C., and De Grandpré, L. 1997. Fine-root dynamics in mixed boreal conifer – broad-leafed forest stands at different successional stages after fire. Canadian Journal of Forest Research **27**(3): 304-314. doi:10.1139/x96-170.

Fisher, R.F., and Binkley, D. 2000. Ecology and management of forest soils. 3rd Edition. John Wiley & Sons Inc., New York, NY, USA.

Fitter, A.H. 1986. The topology and geometry of plant root systems: Influence of watering rate on root system topology in Trifolium pratense. Annals of Botany **58**(1): 91-101.

Gastaldello, P., Ruel, J.-C., and Paré, D. 2007. Micro-variations in yellow birch (*Betula alleghaniensis*) growth conditions after patch scarification. Forest Ecology and Management **238**(1-3): 244-248. doi:10.1016/j.foreco.2006.10.023.

Grossnickle, S.C. 2005. Importance of root growth in overcoming planting stress. New Forests **30**: 273–294. doi:10.1007/s11056-004-8303-2.

Hallsby, G., and Orlander, G. 2004. A comparison of mounding and inverting to establish Norway spruce on podzolic soils in Sweden. Forestry **77**(2): 107-117. doi:10.1093/forestry/77.2.107.

Hawkins, B.J., and Metcalfe, R.J. 2008. Response of Douglas-fir and amabilis fir to split-root nutrition with inorganic and organic nitrogen. Trees - Structure and Function **22**(3): 329-335. doi:10.1007/s00468-007-0188-1.

Heineman, J.L., Bedford, L., and Sword, D. 1999. Root system development of 12-year-old white spruce (*Picea glauca* [Moench] Voss) on a mounded subhygric-mesic site in northern interior British Columbia. Forest Ecology and Management **123**(2/3): 167-177. doi:10.1016/S0378-1127(99)00022-5.

Hodge, A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytologist **162**(1): 9-24. doi:10.1111/j.1469-8137.2004.01015.x.

IUSS Working Group WRB. 2006. World reference base for soil resources. World Soil Resources Reports No. 103. International Union of Soil Sciences (IUSS) and Food and agriculture organization of the United Nations (FAO), Rome, Italy. Available from ftp://ftp.fao.org/agl/agll/docs/wsrr103e.pdf [accessed 15 March 2013].

Kabba, B.S., Knight, J.D., and Van Rees, K.C.J. 2007. Growth of hybrid poplar as affected by dandelion and quackgrass competition. Plant and Soil **298**(1-2): 203-217. doi:10.1007/s11104-007-9355-9.

Kabrick, J.M., Dey, D.C., Van Sambeek, J.W., Wallendorf, M., and Gold, M.A. 2005. Soil properties and growth of swamp white oak and pin oak on bedded soils in the lower Missouri River floodplain. Forest Ecology and Management : **204**: 315-327. doi:10.1016/j.foreco.2004.09.014.

Kjønaas, O.J. 1999. Factors affecting stability and efficiency of ion exchange resins in studies of soil nitrogen transformation. Communications in Soil Science and Plant Analysis **30**(17-18): 2377-2397. doi:10.1080/00103629909370380.

Knapp, B.O., Wang, G.G., and Walker, J.L. 2008. Relating the survival and growth of planted longleaf pine seedlings to microsite conditions altered by site preparation treatments. Forest Ecology and Management **255**(11): 3768-3777.

Knapp, B.O., Wang, G.G., Walker, J.L., and Cohen, S. 2006. Effects of site preparation treatments on early growth and survival of planted longleaf pine (*Pinus palustris* Mill.) seedlings in North Carolina. Forest Ecology and Management **226**(1-3): 122-128. doi:10.1016/j.foreco.2006.01.029.

Leirós, M.C., Trasar-Cepeda, C., Seoane, S., and Gil-Sotres, F. 1999. Dependence of mineralization of soil organic matter on temperature and moisture. Soil Biology and Biochemistry **31**(3): 327-335. doi:10.1016/S0038-0717(98)00129-1.

Löf, M., Dey, D.C., Navarro, R.M., and Jacobs, D.F. 2012. Mechanical site preparation for forest restoration. New Forests **43**(5-6): 825-848. doi:doi:10.1007/s11056-012-9332-x.

Löf, M., and Welander, N.T. 2004. Influence of herbaceous competitors on early growth in direct seeded *Fagus sylvatica* L. and *Quercus robur* L. Annals of Forest Science **61**(781-788).

Londo, A.J., and Mroz, G.D. 2001. Bucket mounding as a mechanical site preparation technique in wetlands. Northern Journal of Applied Forestry **18**(1): 7-13.

Luoranen, J., Rikala, R., Konttinen, K., and Smolander, H. 2006. Summer planting of Picea abies container-grown seedlings: Effects of planting date on survival, height growth and root egress. Forest Ecology and Management **237**(1-3): 534-544. doi:doi:10.1016/j.foreco.2006.09.073.

Makita, N., Hirano, Y., Mizoguchi, T., Kominami, Y., Dannoura, M., Ishii, H., Finér, L., and Kanazawa, Y. 2011. Very fine roots respond to soil depth: Biomass allocation, morphology, and physiology in a broad-leaved temperate forest. Ecological Research **26**(1): 95-104. doi:10.1007/s11284-010-0764-5.

Maynard, D.G., Kalra, Y.P., and Crumbaugh, J.A. 2007. Nitrate and exchangeable ammonium nitrogen. *In* Soil sampling and methods of analysis (second edition). *Edited by* M. R. Carter, and E. G. Gregorich. CRC Press, Taylor & Francis Group, Boca Raton, FL, USA. pp. 71-80.

Messier, C., Coll, L., Poitras-Larivière, A., Bélanger, N., and Brisson, J. 2009. Resource and non-resource root competition effects of grasses on early- versus late-successional trees. Journal of Ecology **97**(3): 548-554. doi:10.1111/j.1365-2745.2009.01500.x.

Messier, C., Parent, S., and Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. Journal of Vegetation Science **9**(4): 511-520. doi:10.2307/3237266.

Mitchell, C.P., Stevens, E.A., and Watters, M.P. 1999. Short-rotation forestry - operations, productivity and costs based on experience gained in the UK. Forest Ecology and Management **121**(1-2): 123-136. doi:10.1016/S0378-1127(98)00561-1.

Morris, L.A., and Lowery, R.F. 1988. Influence of site preparation on soil conditions affecting stand establishment and tree growth. Southern Journal of Applied Forestry **12**: 170-178.

Moukoumi, J., Farrell, R.E., Van Rees, K.J.C., Hynes, R.K., and Bélanger, N. 2012. Intercropping *Caragana arborescens* with *Salix miyabeana* to satisfy nitrogen demand and maximize growth. BioEnergy Research **5**(3): 719-732. doi:10.1007/s12155-012-9181-7.

Nadeau, L.B., and Pluth, D.J. 1997. Spatial distribution of lodgepole pine and white spruce seedling roots 10 years after deep tillage of a Gray Luvisol. Canadian Journal of Forest Research **27**(10): 1606-1613. doi:10.1139/x97-125.

Newton, P.F., and Amponsah, I.G. 2006. Systematic review of short-term growth responses of semi-mature black spruce and jack pine stands to nitrogen-based fertilization treatments. Forest Ecology and Management **237**(1–3): 1-14. doi:10.1016/j.foreco.2006.10.009.

Nilsson, U., and Örlander, G. 1999. Vegetation management on grass-dominated clearcuts planted with Norway spruce seedlings in southern Sweden. Canadian Journal of Forest Research **29**(7): 1015-1026. doi:10.1139/x99-071.

Nordborg, F., Nilsson, U., Gemmel, P., and Örlander, G. 2006. Carbon and nitrogen stocks in soil, trees and field vegetation in conifer plantations 10 years after deep soil cultivation and patch scarification. Scandinavian Journal of Forest Research **21**(5): 356-363.

Nordborg, F., Nilsson, U., and Örlander, G. 2003. Effects of different soil treatments on growth and net nitrogen uptake of newly planted *Picea abies* (L.) Karst. seedlings. Forest Ecology and Management **180**(1-3): 571-582.

Novoplansky, A. 2009. Picking battles wisely: plant behaviour under competition. Plant, Cell & Environment **32**(6): 726-741. doi:10.1111/j.1365-3040.2009.01979.x.

Örlander, G., Egnell, G., and Albrektson, A. 1996. Long-term effects of site preparation on growth in Scots pine. Forest Ecology and Management **86**(1-3): 27-37. doi:10.1016/S0378-1127(96)03797-8.

Örlander, G., Gemmel, P., and Hunt, J. 1990. Site preparation: a Swedish overview. Forestry Canada and BC Ministry of Forests, Victoria, BC, Canada, 61 p. Available from http://www.for.gov.bc.ca/hfd/pubs/docs/Frr/Frr105.htm [accessed 15 Mach 2013].

Paré, D., Bergeron, Y., and Longpré, M.-H. 2001. Potential productivity of aspen cohorts originating from fire, harvesting, and tree-fall gaps on two deposit types in northwestern Quebec. Canadian Journal of Forest Research **31**: 1067-1073. doi:10.1139/x01-036.

Paré, D., and Bernier, B. 1989. Origin of the phosphorus deficiency observed in declining sugar maple stands in the Quebec Appalachians. Canadian Journal of Forest Research **19**(1): 24-34. doi:10.1139/x89-004.

Pennanen, T., Heiskanen, J., and Korkama, T. 2005. Dynamics of ectomycorrhizal fungi and growth of Norway spruce seedlings after planting on a mounded forest clearcut. Forest Ecologz and Management **213**: 243-252. doi:doi:10.1016/j.foreco.2005.03.044.

Périnet, P., Gagnon, H., and Morin, S. 2001. Liste des clones recommandés de peuplier hybride par sous-région écologique au Québec. Ministère des Ressources naturelles du Québec, Direction de la recherche forestière, Québec, QC, Canada.

Qian, P., and Schoenau, J.J. 2002. Practical applications of ion exchange resins in agricultural and environmental soil research. Canadian Journal of Soil Science **82**(1): 9-21. doi:10.4141/S00-091.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/ [accessed 15 July 2013].

Raison, R.J., Connell, M.J., and Khanna, P.K. 1987. Methodology for studying fluxes of soil mineral-N *in situ*. Soil Biology and Biochemistry **19**(5): 521-530. doi:10.1016/0038-0717(87)90094-0.

Rose, D.A. 1983. The description of the growth of root systems. Plant and Soil **75**: 405-415.

Ross, S.M., and Malcolm, D.C. 1982. Effects of intensive forestry ploughing practices on an upland heath soil in southeast Scotland. Forestry **55**: 155-171.

Saxton, K.E., Rawls, W.J., Romberger, J.S., and Papendick, R.I. 1986. Estimating generalized soil-water characteristics from texture. Soil Science Society of America Journal **50**(4): 1031-1036. doi:10.2136/sssaj1986.03615995005000040039x. (Soil texture calculations available from http://www.pedosphere.ca/resources/bulkdensity/).

Schenk, H.J., Callaway, R.M., and Mahall, B.E. 1999. Spatial root segregation: are plants territorial? Advances in Ecological Research **28**: 145-180. doi:10.1016/S0065-2504(08)60032-X.

Searle, S.R., Casella, G., and McCulloch, C.E. 1992. Variance Components. John Wiley and Sons, New York, NY, USA.

Soil Classification Working Group. 1998. The Canadian system of soil classification. Agriculture and Agri-Food Canada, Publication 1646 (Revised), 3rd edition. NRC Research Press, Ottawa, ON, Canada, 187 p. Available from http://sis.agr.gc.ca/cansis/publications/manuals/1998-1646-ed3/intro.html [accessed 15 Mach 2013].

Stettler, R.F., Bradshaw Jr., H.D., Heilman, P.E., and Hinckley, T.M. 1996. Bology of *Populus* and its implications for management and conservation. NRC Research Press, Ottawa, ON, Canada, 542 p. From http://www.nrcresearchpress.com/doi/book/10.1139/9780660165066 [accessed 21 March 2013].

Strong, W.L., and La Roi, G.H. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Canadian journal of forest research **13**(6): 1164-1173.

Strong, W.L., and La Roi, G.H. 1985. Root density-soil relationships in selected boreal forests of central Alberta, Canada. Forest Ecology and Management **12**(3-4): 233-251. doi:10.1016/0378-1127(85)90093-3.

Strong, W.L., and La Roi, G.H. 1988. Use of soil horizons as ecological sampling units. Canadian Journal of Soil Science **68**(1): 151-155. doi:10.4141/cjss88-014.

Sutton, R.F. 1993. Mounding site preparation: a review of European and North American experience. New Forests **7**(2): 151-192. doi:10.1007/BF00034198.

Teskey, R.O., and Hinckley, T.M. 1981. Influence of temperature and water potential on root growth of white oak. Physiologia Plantarum **52**(3): 363-369. doi:10.1111/j.1399-3054.1981.tb06055.x.

Van Rees, K.C.J. 1997. Rooting patterns of boreal tree species. Final report submitted to: The Prince Albert Model Forest Association, Canadian Forest Service, Prince Albert, SK, Canada, 52 p. Available from http://www.pamodelforest.sk.ca/pubs/PAMF5000.pdf [accessed 15 March 2013].

Wolfinger, R., Tobias, R., and Sall, J. 1994. Computing Gaussian Likelihoods and Their Derivatives for General Linear Mixed Models. SIAM Journal on Scientific Computing **15**: 1294-1310.

Wolken, J.M., Landhäusser, S.M., Lieffers, V.J., and Dyck, M.F. 2010. Differences in initial root development and soil conditions affect establishment of trembling aspen and balsam poplar seedlings. Botany **88**(3): 275-285.

Wood, T., Bormann, F.H., and Voigt, G.K. 1984. Phosphorus cycling in a northern hardwood forest: biological and chemical control. Science **223**(4634): 391-393. doi:10.1126/science.223.4634.391

Table 1. Typical vertical soil profiles of the two soil treatments (mechanical soil preparation by mounding, and the unprepared control) describing the soil layer types and their thickness. Soil layers are presented from top to bottom in the table as they are found from the soil surface down to deeper horizons in the tree's immediate soil environment.

Soil layer	Thickness (cm)	SE
Mounding		
Upper mineral *	16.0	1.9
Buried organic layer	7.5	0.6
Lower mineral	7.8	2.2
Max. depth reached by roots †	31.3	2.4
Unprepared		
Surface organic layer	10.8	1.3
Lower mineral	10.5	1.9
Max. depth reached by roots	21.3	1.4

* The upper mineral layer in the tree's immediate environment is not as thick as the highest point of the mound since the tree is planted on its side.

† Maximum depth reached by roots corresponds to the deepest location of a root as observed in the field root excavations (*n* = 8).

Table 2. Mean number of proximal roots per tree in mounds compared to unprepared soils, all soil layers combined but for different root diameter classes.

	Nb. roots tree^{-1} *	SE †	P-value ‡
All diameter classes			
Mounding	35.0	2.3	0.006
Unprepared	25.5	2.5	
0-2 mm			
Mounding	16.8	1.9	0.25
Unprepared	13.6	2.0	
2-10 mm			
Mounding	12.2	0.9	0.054
Unprepared	9.6	0.9	
11-20 mm			
Mounding	4.9	0.3	<.0001
Unprepared	2.0	0.3	
21-30 mm			
Mounding	0.96	0.2	0.001
Unprepared	0.095	0.2	

* Root numbers are means per tree from 24 (mounding) and 21 (unprepared) excavated hybrid poplars at 8 sites.

† SE = standard error.

‡ P-values were produced by mixed analyses of variance comparing mounding with unprepared soil.

Table 3. Detailed results of the mixed ANOVA comparing roots and soil data by soil treatment and soil layer.

Analyzed variable	Source of variation *	df	SSE	MSE	% variance †	F-value	P-value
Number of roots							
	Fixed effects						
	Soil treatment & layer & diameter class	19	44.79	2.357	92.9	13.04	< 0.0001
	Random effects						
	Site	7	2.254×10^{-11}	3.220×10^{-12}	1.27×10^{-10}		
	Plot	133	1.265	0.009515	0.375		
	Residuals	296	50.60	0.1709	6.74		
	Total	455					
Resin-adsorbed N							
	Fixed effects						
	Soil treatment & layer	4	0.005158	0.0012894	94.4	17.28	< 0.0001
	Random effects						
	Site	7	2.270×10^{-12}	3.243×10^{-13}	2.37×10^{-8}		
	Plot	28	0.0004850	1.732×10^{-5}	1.29		
	Residuals	72	0.004274	5.937×10^{-5}	4.35		
	Total	111					
Net mineralized N							
	Fixed effects						
	Soil treatment & layer	4	0.0875	0.021876	76.8	3.355	0.0125
	Random effects						
	Site	7	5.663×10^{-12}	8.090×10^{-13}	2.84×10^{-9}		
	Plot	28	0.01700	0.0006073	2.13		
	Residuals	72	0.4320	0.00600	21.1		
	Total	111					
Total net mineralized N							
	Fixed effects						
	Soil treatment & layer	4	1589	397.1	86.6	6.516	< 0.0001
	Random effects						
	Site	7	19.40	2.771	0.604		
	Plot	28	95.19	3.40	0.741		
	Residuals	72	3980	55.28	12.1		
	Total	111					

* Soil treatment & layer = a meta-variable with 5 levels, created by combining “soil treatment” (mounding, unprepared) with “soil layer”. For roots, it also included diameter class. See Data analysis, in Methods.

† The % variance is the proportion of the total variance provided by a given source of variation.

Table 4. Soil temperature measured continuously with data-logging sensors during June-August.

	Mean *	SE †
Soil temperature (°C), overall		
Mounding	15.4	2.4
Unprepared	14.5	1.8
P-value	0.15	
Soil temperature (°C), Day ‡		
Mounding	15.8	3.1
Unprepared	15.6	1.8
P-value	0.56	
Soil temperature (°C), Night ‡		
Mounding	15.1	1.6
Unprepared	13.4	1.3
P-value	0.006	

* Mean = average value for three depths (2, 10, and 20 cm) from 15 trees at two sites.

† SE = standard error.

‡ Day = 07:00 to 19:00, Night = 21:00 to 05:00.

Table 5. Aboveground measurements for 3-yr-old hybrid poplars in the two soil treatments.

		Mounding	Unprepared
Height, cm	mean	273	171
	SE †	18	17
	P-value	<0.0001	
mid-DBH, mm *	mean	27.8	14.7
	SE	3.7	1.6
	P-value	<0.0001	
height:root	mean	1.5	2.7
	SE	0.3	0.3
	P-value	0.015	

* mid-DBH = diameter at breast height taken 65 cm above the ground.

† SE = standard error.

Table 6. Correlations on rank (Spearman's rho, ρ) between root characteristics (per tree) and other soil and tree variables.

Variable 1	Variable 2	Spearman's Rho	Prob>|Rho|
Nb. of proximal roots	Mid-DBH *	0.4862	0.0007
	Total tree height	0.5598	<.0001
Average proximal root diameter	Mid-DBH	0.2318	0.1255
	Total tree height	0.1799	0.2371
	Soil temperature	0.1043	0.4952
	Net mineralized N	-0.5766	<.0001
Shoot: root ratio	Net mineralized N	-0.3006	0.0448
Nb. of proximal roots in diameter class			
0-2 mm	Total tree height	0.3591	0.0154
	No. of proximal roots per tree	0.8548	<.0001
2-10 mm	Mid-DBH	0.3006	0.0448
	Average proximal root diameter	0.3161	0.0344
	Total tree height	0.3723	0.0118
	No. of proximal roots	0.6934	<.0001
11-20 mm	Mid-DBH	0.7710	<.0001
	Total tree height	0.6800	<.0001
	Soil temperature	0.7881	<.0001
21-30 mm	Mid-DBH	0.6605	<.0001
	Total tree height	0.6333	<.0001
	Soil temperature	0.5405	0.0001
	Resin-adsorbed N	0.3447	0.0204

* Mid-DBH: diameter at breast height taken 65 cm above the ground.

FIGURE CAPTIONS

Figure 1. Schematic representation of the mounding process (inspired by Sutton 1993). 1) A portion of the undisturbed soil – covered with competing herbaceous and woody vegetation – is dug out; 2) the dugout soil material is inverted; and 3) placed nearby over the undisturbed organic layer, thus covering and killing the competing vegetation. The tree is planted on the hillside of this mound.

Figure 2. Number of hybrid poplar proximal roots per cm of soil depth per tree, among four root diameter classes, for the two soil treatments (mounding, unprepared), and for different soil layers. Values are means across eight sites and error bars are standard errors. Depth and thickness of soil layers are based on measurements of the vertical soil profile made during root excavations. Different letters indicate a significant difference at $\alpha = 0.05$ between bars (each bar of the graph is a combination of soil treatment × soil layer × diameter class, and all combinations are compared at the same time).

Figure 3. Different aspects of soil N dynamics by soil treatment (mounding, unprepared) and soil layer (identified by depth and soil material). A) Concentrations (g m^{-2}) of total inorganic N, i.e., $[NH_4+NO_3]$-N, adsorbed onto ion-exchange resins. B) Net mineralized N per soil unit mass (g kg^{-1}). Values come from 6-week *in situ* burials (A) or incubations (B). C) Total net mineralized N (g) in the rooting volume. This volume was estimated for a cylindrical soil volume of fixed surface area (a circle of 50-cm radius around the tree) and a depth determined by the position in the soil profile of the deepest proximal roots (see Table 1 for depths and thickness of soil layers). Values are means across eight sites and error bars are standard errors. Different letters indicate a significant difference at $\alpha = 0.05$ between bars (each bar is a combination of soil treatment × soil layer, and all five combinations are compared at the same time in a given graph).

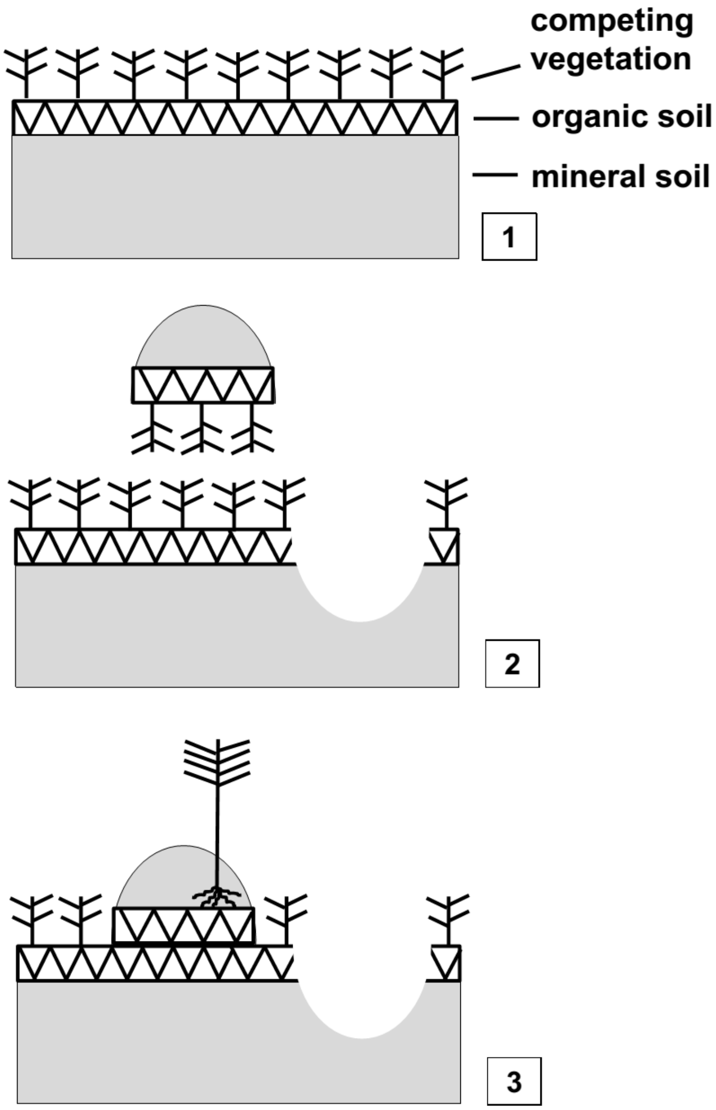

Figure 1. Schematic representation of the mounding process (inspired by Sutton 1993). 1) A portion of the undisturbed soil – covered with competing herbaceous and woody vegetation – is dug out; 2) the dugout soil material is inverted; and 3) placed nearby over the undisturbed organic layer, thus covering and killing the competing vegetation. The tree is planted on the hillside of this mound.

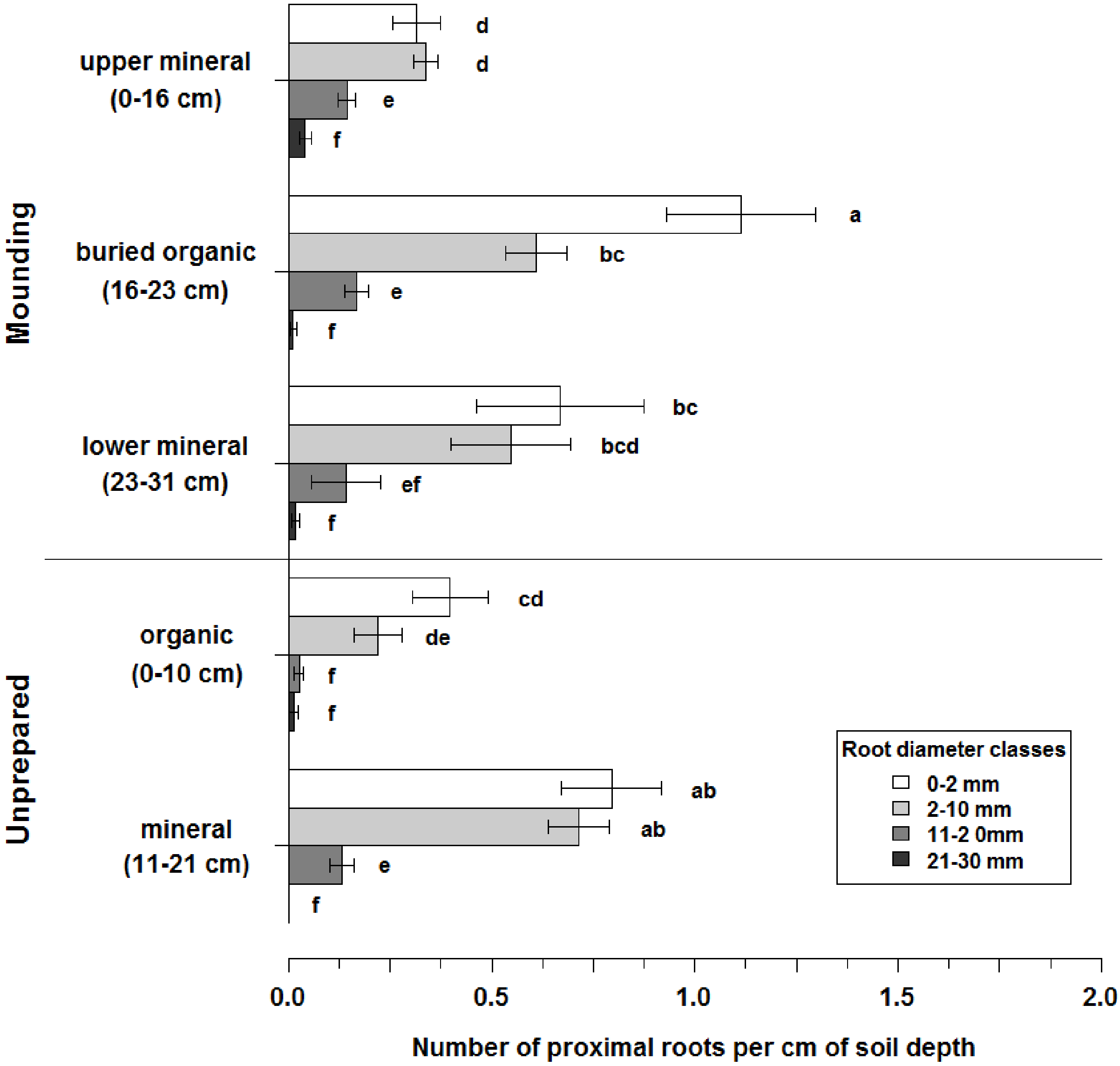

Figure 2. Number of hybrid poplar proximal roots per cm of soil depth per tree, among four root diameter classes, for the two soil treatments (mounding, unprepared), and for different soil layers. Values are means across eight sites and error bars are standard errors. Depth and thickness of soil layers are based on measurements of the vertical soil profile made during root excavations. Different letters indicate a significant difference at α = 0.05 between bars (each bar of the graph is a combination of soil treatment × soil layer × diameter class, and all combinations are compared at the same time).

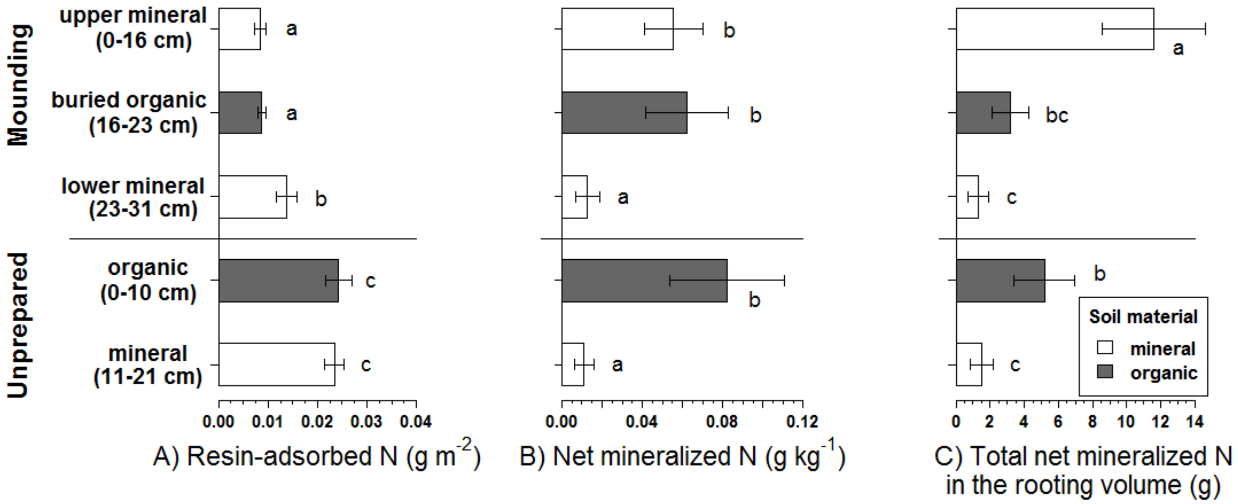

Figure 3. Different aspects of soil N dynamics by soil treatment (mounding, unprepared) and soil layer (identified by depth and soil material). A) Concentrations (g m^{-2}) of total inorganic N, i.e., [NH_4+NO_3]-N, adsorbed onto ion-exchange resins. B) Net mineralized N per soil unit mass (g kg^{-1}). Values come from 6-week *in situ* burials (A) or incubations (B). C) Total net mineralized N (g) in the rooting volume. This volume was estimated for a cylindrical soil volume of fixed surface area (a circle of 50-cm radius around the tree) and a depth determined by the position in the soil profile of the deepest proximal roots (see Table 1 for depths and thickness of soil layers). Values are means across eight sites and error bars are standard errors. Different letters indicate a significant difference at α = 0.05 between bars (each bar is a combination of soil treatment × soil layer, and all five combinations are compared at the same time in a given graph).